

EARLY ANIMALS

Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals

Ilya Bobrovskiy^{1*}, Janet M. Hope¹, Andrey Ivantsov², Benjamin J. Nettersheim³, Christian Hallmann^{3,4}, Jochen J. Brocks^{1*}

The enigmatic Ediacara biota (571 million to 541 million years ago) represents the first macroscopic complex organisms in the geological record and may hold the key to our understanding of the origin of animals. Ediacaran macrofossils are as “strange as life on another planet” and have evaded taxonomic classification, with interpretations ranging from marine animals or giant single-celled protists to terrestrial lichens. Here, we show that lipid biomarkers extracted from organically preserved Ediacaran macrofossils unambiguously clarify their phylogeny. *Dickinsonia* and its relatives solely produced cholesteroloids, a hallmark of animals. Our results make these iconic members of the Ediacara biota the oldest confirmed macroscopic animals in the rock record, indicating that the appearance of the Ediacara biota was indeed a prelude to the Cambrian explosion of animal life.

The Ediacara biota remains one of the greatest mysteries in paleontology. Members of this assemblage were initially described as animals (1, 2); however, as collections grew, it became apparent that Ediacaran fossils and their body plans are difficult to compare with modern phyla (3, 4). A major complication for the study of Ediacaran organisms is their soft-bodied nature and particular mode of preservation, rarely found in younger fossils. Thus, the interpretation of various members of the Ediacara biota has crossed several Kingdoms and Domains, ranging from bacterial colonies (5), marine fungi (6), lichens (7), and giant protists (8, 9) to stem-group animals and crown-group Eumetazoa (4, 10, 11). The recent general consensus is that these fossils are polyphyletic (12, 13): At least some members of the Ediacara biota are almost unanimously interpreted as bilaterian animals (*Kimberella*) (14, 15), whereas others are confidently ascribed to giant protozoa (*Palaeopascichmus*) (16). *Beltanelliformis*—although previously interpreted as bacteria, benthic and planktonic algae, as well as different animals—is now recognized as a spherical colony of cyanobacteria on the basis of their biomarker content (17). The affinity of most other Ediacarans, however, remains controversial, even at the Kingdom level (4). Most recently, arguments surrounding these fossils have centered on lichens, giant protists, and stem- or crown-group Metazoa.

Whereas the lichen hypothesis (7) requires an implausible reinterpretation of the habitat of the Ediacara biota from a marine to a conti-

mental depositional environment (18), for many Ediacaran fossils, including dickinsoniids, it currently seems impossible to distinguish between giant protist and metazoan origins (4, 19). Some Ediacaran fossils, such as *Palaeopascichmus*, were likely giant unicellular eukaryotes (protists) (16), which means that in contrast to modern ecosystems, these organisms were present and sometimes extremely abundant in shallow-water Ediacaran habitats (20). Features of dickinsoniids such as “quilting” patterns, the inferred absence of dorso-ventral differentiation, and putative external digestion mode were found to be compatible with modern giant protists and hard to reconcile with metazoans (8, 20). Some modern giant protists can be up to 25 cm in size (21). In the absence of metazoan competition, they may have become even larger, possibly providing an explanation for the size range of Ediacaran protistan fossils (8). Some giant protists even have a motile lifestyle, compatible with Ediacaran trace fossils (22) and dickinsoniid “footprints” (15). For dickinsoniids, the absence of evidence for a mouth and gut, perceived absence of bilateral symmetry, and possible external digestion are all consistent with a protistan origin. However, all of the above characteristics are also compatible with basal Metazoa such as the Placozoa that are situated at the very base of Eumetazoa (23), whereas rejection of an external digestion mode and acceptance of supposed cephalization (15) may place dickinsoniids even higher on the metazoan tree. The nature of dickinsoniids, and most other Ediacaran fossils, thus remains unresolved.

We applied a new approach (17) to test the lichen, protist, and animal hypotheses by studying biomarkers extracted from organically preserved dickinsoniids. Hydrocarbon biomarkers are the molecular fossils of lipids and other biological compounds. Encased in sedimentary rock, biomarkers may retain information about their biological origins for hundreds of millions of

years. For instance, hopanes are the hydrocarbon remains of bacterial hopanepolyols, whereas saturated steranes and aromatic steroids are diagenetic products of eukaryotic sterols. The most common sterols of Eukarya possess a cholesteroloid, ergosteroid, or stigmateroid skeleton with 27, 28, or 29 carbon atoms, respectively. These C₂₇ to C₂₉ sterols, distinguished by the alkylation pattern at position C-24 in the sterol side chain, function as membrane modifiers and are widely distributed across extant Eukarya, but their relative abundances can give clues about the source organisms (24).

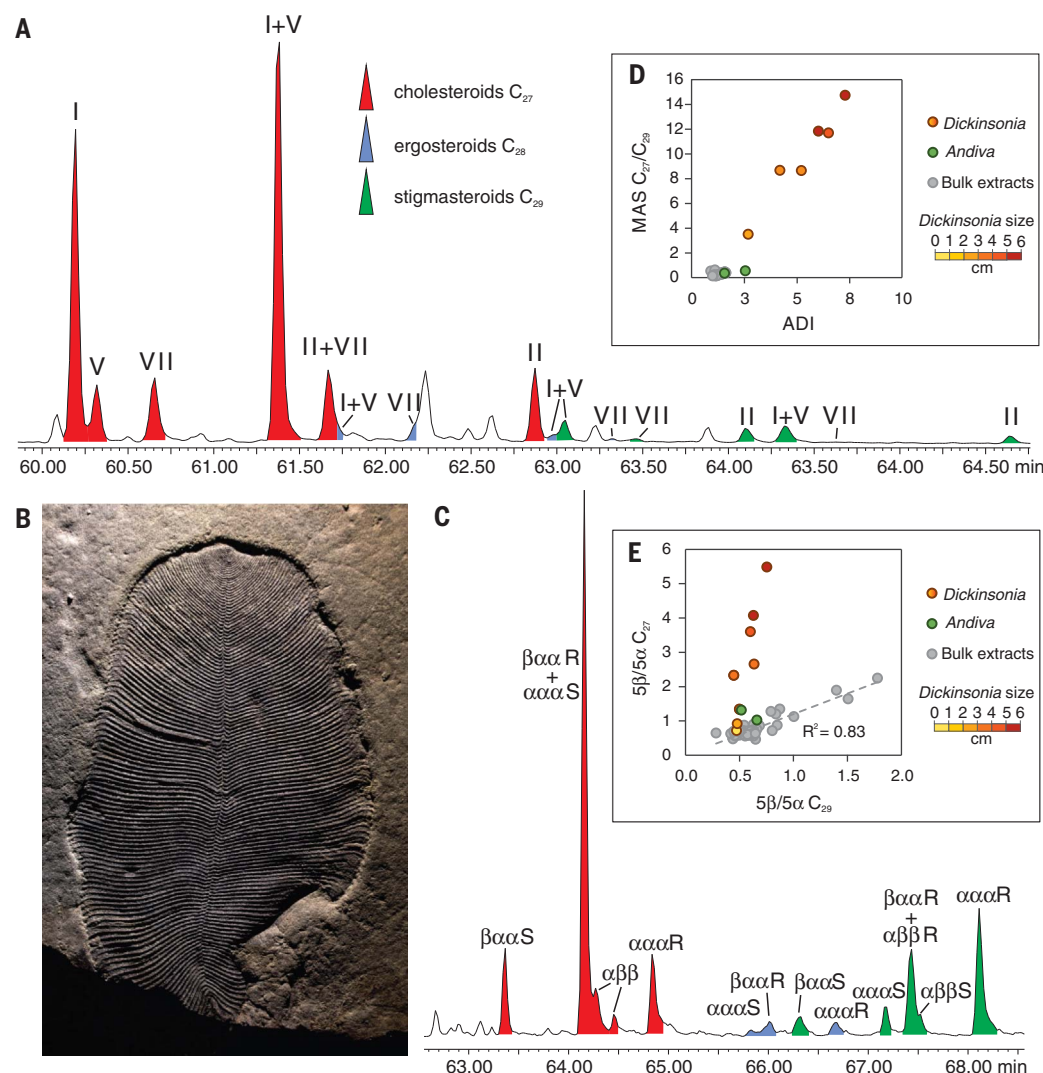
Apart from *Dickinsonia* (Fig. 1B), which is one of the most recognizable Ediacaran fossils, dickinsoniids include *Andiva* (Fig. 1C and fig. S1), *Vendia*, *Yorgia*, and other flattened Ediacaran organisms with segmented metameric bodies and a median line along the body axes, separating the “segments.” The specimens for this study were collected from two surfaces in the Lyamtsa (*Dickinsonia*) and Zimmie Gory (*Andiva*) localities of the Ediacara biota in the White Sea region (Russia). Both *Dickinsonia* and *Andiva* are preserved in negative hyporelief on the sole of sandstones with microbial mat impressions and consist of a thin (up to ~3 μm) film of organic matter. The organic matter was detached from the rock surface (fig. S1) and extracted for hydrocarbon biomarkers under strict exclusion of contamination (materials and methods). Much thinner organic films covering the surfaces around *Andiva* fossils from the Zimmie Gory locality were extracted as well, providing a background signal coming from associated microbial mats. Investigation of biomarker composition of surrounding surfaces and enclosing sedimentary rocks allowed us not only to subtract the background signal but also to make sure that the biomarker signal from the fossils is not contaminated (supplementary text). We analyzed biomarkers using gas chromatography-mass spectrometry (materials and methods).

The deposits immediately above and below *Dickinsonia* are characterized by a monoaromatic steroid distribution of 10.6 to 11.9% cholesteroloids, 13.4 to 16.8% ergosteroids, and 71.3 to 76.0% stigmateroids, which is consistent with the general steroid distribution of sediments at the Lyamtsa locality (Fig. 1). The strong stigmateroid predominance is typical for the Ediacaran period and presumably related to green algae (Chlorophyta) inhabiting benthic mats or the water column (25). In these and all other Ediacaran sediment samples from the White Sea region, the carbon-number distribution of saturated steranes is nearly identical to the distribution of monoaromatic steroid homologs and always dominated by green algal stigmateroids (Table 1). By contrast, biomarkers extracted from the isolated organic matter of the largest *Dickinsonia* specimen had a monoaromatic steroid distribution of 93% cholesteroloids, 1.8% ergosteroids, and 5.2% stigmateroids (Fig. 1A and Table 1). A general trend of increasing monoaromatic cholesteroloid abundance from 84.8 to 93.0% from the smaller to the larger *Dickinsonia* specimens

¹Research School of Earth Sciences, Australian National University, Canberra ACT 2601, Australia. ²Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow 117997, Russia. ³Max Planck Institute for Biogeochemistry, Jena 07745, Germany. ⁴MARUM—Center for Marine Environmental Sciences, University of Bremen, Bremen 28359, Germany. *Corresponding author. Email: ilya.bobrovskiy@anu.edu.au (I.B.); jochen.brocks@anu.edu.au (J.J.B.)

Fig. 1. Biomarkers from organically preserved *Dickinsonia*.

(A) Mass/charge ratio 253 selected ion recording chromatogram showing the distribution of monoaromatic steroids (MAS) of the solvent extract of a large *Dickinsonia* specimen (*Dickinsonia*-2; 5.5 cm width). (B) Organically preserved *Dickinsonia* from the Lyamtsa locality (*Dickinsonia*-2). (C) Metastable reaction monitoring chromatogram showing the sum of C_{27-29} sterane traces of *Dickinsonia*-2. $\alpha\beta\beta = 5\alpha(H)$, $14\beta(H)$, $17\beta(H)$ (and correspondingly for $\alpha\alpha\alpha$ and $\beta\alpha\alpha$); S and R indicate isomerization at position C-20. (D) Relationship between the MAS $C_{27}/MAS C_{29}$ ratio and the Animal Decomposition Index (ADI) = $(C_{27} 5\beta/5\alpha)/(C_{29} 5\beta/5\alpha)$ in *Dickinsonia* ($n = 6$ samples), *Andiva* ($n = 2$ samples), and bulk rock extracts from the Lyamtsa and Zimmie Gory localities ($n = 32$ samples). Only samples with detectable MAS were used in the plot. ADI is a measure of the quantity of sterols that decomposed in the anaerobic microenvironment of an animal carcass relative to normal sterol decomposition within the background sediment. ADI ≈ 1 indicates that cholesterol and stigmateroids underwent alteration in the same diagenetic environment consistent with the absence of animal tissue. ADI > 1 indicates contribution of animal sterols to the biomarker signal. (E) Relationship between the $5\beta/5\alpha$ sterane isomer ratio for cholestane (C_{27}) and stigmastane (C_{29}) in *Dickinsonia* ($n = 8$ samples), *Andiva* ($n = 2$ samples), and bulk rock extracts from the Lyamtsa and Zimmie Gory localities ($n = 54$ samples). $5\beta/5\alpha = (\beta\alpha\alpha 20R + \alpha\alpha\alpha 20S)/\alpha\alpha\alpha 20R$. MAS structures: I = $5\beta(H)10\beta(CH_3)$, II = $5\alpha(H)10\beta(CH_3)$, V = $5\beta(CH_3)10\beta(H)$, and VII = $5\alpha(CH_3)10\alpha(H)$.



(Fig. 1D) reflects decreasing contribution of the green algal background signal (fig. S2).

The striking abundance of cholesterol in *Dickinsonia* is corroborated by an unusual sterane isomer distribution. In sediments surrounding the fossils in Lyamtsa and Zimmie Gory localities, the ratio of 5β over 5α stereoisomers for all steranes is generally near the equilibrium diagnostic for abiological isomerization (average $5\beta/5\alpha = 0.65 \pm 0.26$, $n = 54$ samples) (Fig. 1, D and E). By contrast, in the fossils, $5\beta/5\alpha$ of cholestane is markedly elevated—up to 5.5 in *Dickinsonia* (Table 1 and Fig. 1, C, D, and E)—values that are generated through strictly anaerobic microbial activity (26, 27), such as during the decay of carcasses. Although the gut flora of some mammals is known to produce 5β -stanols (precursors of 5β -steranes) (28), high relative abundances of these molecules in some background sediments (Fig. 1E) and macroalgae (17) from the White Sea contests the otherwise exciting possibil-

ity that 5β -steranes originated from *Dickinsonia*'s gut microbiota (supplementary text). 5β ergosteranes and stigmateranes in the *Dickinsonia* extracts are not elevated (Table 1), demonstrating that they are ultimately not derived from dickinsoniids but from the underlying microbial mat or surrounding sediment (fig. S2). On the basis of these steroid homolog and isomer patterns, we compute that the sterols of living *Dickinsonia* consisted of at least 99.7% cholesterol (supplementary text). Within analytical precision, it is impossible to exclude that *Dickinsonia* produced traces of ergosteroids (up to 0.23%) or stigmateroids (up to 0.07%). Such sterols, if present, may be derived from the organism itself but could also represent dietary uptake or contributions from symbionts.

Biomarker signatures of *Andiva* specimens from the Zimmie Gory locality are less well differentiated from the microbial mat background signal and do not display a clear elevation of

cholesteroids relative to the background (Table 1). Yet even in these fossils, $5\beta/5\alpha$ ratios for cholestanes are much higher ($5\beta/5\alpha = 1.02$ to 1.31) when compared with ergosteranes and stigmateranes from the fossil extract ($5\beta/5\alpha = 0.52$ to 0.66) and the surrounding mat ($5\beta/5\alpha = 0.65$ to 0.81) (Table 1). On the basis of these values, we can compute a conservative minimum C_{27} sterol content of 88.1% for *Andiva* (supplementary text).

Using the remarkable steroid patterns of the fossils, it is possible to test the position of dickinsoniids on the phylogenetic tree. Lichen-forming fungi only produce ergosteroids, and even in those that host symbiotic algae, ergosteroids remain the major sterols (29, 30). *Dickinsonia* contained no or a maximum of only 0.23% ergosteroids, conclusively refuting the lichen hypothesis (7). The groups of rhizarian protists that include gigantic representatives (Gromiidae, Xenophyophorea, and other Foraminifera) and their retarian relatives all produce a complex

Table 1. Steroid distributions in *Dickinsonia* and *Andiva* extracts. C₃₀ steranes are only represented by 24-isopropylcholestanes. 5β/5α = (βαα 20R + ααα 20S)/ααα 20R. ADI = (C₂₇ 5β/5α)/(C₂₉ 5β/5α) (Fig. 1). Only the I and V monoaromatic steroid isomers (nomenclature provided in Fig. 1) were used for all computations because they display the least coelution with other peaks on the chromatogram. Numbers in parentheses are standard deviation values, and numbers in brackets next to zero values represent the detection limit (the maximum of a given compound that may be present when not detected). n/a, not applicable; dashes indicate not measurable.

Sample	Locality	Size (width, cm)	Saturated steranes							Monoaromatic steroids				
			C ₂₇ (%)	C ₂₈ (%)	C ₂₉ (%)	C ₃₀	C ₂₇ 5β/5α	C ₂₈ 5β/5α	C ₂₉ 5β/5α	ADI	C ₂₇ (%)	C ₂₈ (%)	C ₂₉ (%)	C ₂₇ /C ₂₉
<i>Dickinsonia</i> -1	Lyamtsa	6.0	48.1 (1.3)	5.7 (0.2)	45.8 (1.2)	0.4 (0.04)	3.61 (0.21)	0.52 (0.34)	0.60 (0.06)	6.01 (0.67)	92.4 (2.5)	2.1 (0.1)	5.5 (0.3)	11.84 (0.93)
<i>Dickinsonia</i> -2	Lyamtsa	5.5	63.2 (1.5)	4.9 (0.2)	31.9 (0.8)	0 {0.05}	5.49 (0.28)	0.65 (0.34)	0.75 (0.06)	7.28 (0.65)	93.0 (2.3)	1.8 (0.1)	5.2 (0.3)	14.75 (0.91)
<i>Dickinsonia</i> -3	Lyamtsa	4.5	47.9 (1.5)	6.1 (0.3)	46.0 (1.4)	0 {0.03}	4.08 (0.29)	0.75 (0.34)	0.63 (0.04)	6.50 (0.64)	92.5 (3.2)	2.7 (0.2)	4.8 (0.3)	11.71 (1.41)
<i>Dickinsonia</i> -4	Lyamtsa	4.0	33.4 (2.2)	8.0 (0.7)	58.5 (3.5)	0 {0.08}	2.66 (0.41)	0.97 (0.34)	0.64 (0.08)	4.18 (0.83)	87.9 (6.4)	4.8 (0.7)	7.3 (0.9)	8.67 (1.59)
<i>Dickinsonia</i> -5	Lyamtsa	4.0	44.8 (0.9)	7.6 (0.4)	47.6 (1.0)	0 {0.01}	2.33 (0.10)	0.81 (0.34)	0.45 (0.02)	5.21 (0.32)	91.3 (4.5)	3.6 (0.4)	5.1 (0.5)	8.66 (1.81)
<i>Dickinsonia</i> -6	Lyamtsa	3.5	27.5 (0.7)	9.9 (0.5)	62.6 (1.3)	0 {0.04}	1.34 (0.07)	0.79 (0.34)	0.50 (0.02)	2.67 (0.18)	84.8 (5.7)	3.4 (0.5)	11.8 (1.2)	3.51 (0.80)
<i>Dickinsonia</i> -7	Lyamtsa	1.0	17.2 (1.2)	6.9 (1.2)	75.9 (3.6)	0 {0.18}	0.71 (0.10)	0.22 (0.34)	0.47 (0.05)	1.49 (0.26)	—	—	—	—
<i>Dickinsonia</i> -8	Lyamtsa	2.5	20.5 (1.3)	6.7 (1.2)	72.7 (3.6)	0 {0.10}	0.91 (0.13)	0.26 (0.34)	0.48 (0.05)	1.89 (0.32)	—	—	—	—
<i>Dickinsonia</i> - Sandstone	Lyamtsa	n/a	11.6 (0.3)	8.9 (0.2)	78.9 (1.2)	0.6 (0.04)	0.64 (0.04)	0.85 (0.34)	0.52 (0.02)	1.23 (0.08)	11.9 (1.0)	16.8 (1.5)	71.3 (4.4)	0.17 (0.01)
<i>Dickinsonia</i> - Clay	Lyamtsa	n/a	9.7 (0.3)	7.8 (0.2)	82.0 (1.3)	0.5 (0.03)	0.61 (0.03)	0.71 (0.34)	0.59 (0.02)	1.03 (0.07)	10.6 (0.7)	13.4 (0.9)	76.0 (3.3)	0.2 (0.01)
<i>Andiva</i> -1	Zimnie Gory	8.0	24 (0.4)	10.3 (0.3)	64.3 (0.9)	1.3 (0.1)	1.07 (0.04)	0.76 (0.34)	0.68 (0.02)	1.55 (0.07)	21.5 (0.8)	17.5 (0.7)	61.0 (1.9)	0.36 (0.01)
<i>Andiva</i> -2	Zimnie Gory	4.0	24.9 (1.2)	12.2 (1.2)	61.8 (2.7)	1.0 (0.2)	1.31 (0.15)	0.81 (0.34)	0.52 (0.04)	2.54 (0.36)	29.3 (2.6)	12.6 (1.4)	58.1 (4.5)	0.55 (0.05)
<i>Andiva</i> Mat	Zimnie Gory	n/a	25.8 (1.0)	15.8 (1.0)	57.4 (1.9)	1.0 (0.1)	0.80 (0.07)	0.96 (0.34)	0.65 (0.04)	1.24 (0.13)	18.7 (1.4)	21.4 (1.6)	59.8 (3.5)	0.35 (0.02)
<i>Andiva</i> - Sandstone	Zimnie Gory	n/a	37.5 (1.0)	10.5 (0.3)	51.6 (1.3)	0.5 (0.04)	0.65 (0.04)	0.91 (0.34)	0.61 (0.03)	1.08 (0.08)	25.6 (1.7)	15.7 (1.2)	58.7 (3.4)	0.43 (0.03)
<i>Andiva</i> -Clay	Zimnie Gory	n/a	23.1 (0.5)	9.5 (0.3)	65.9 (1.3)	1.5 (0.02)	0.86 (0.04)	0.84 (0.34)	0.68 (0.02)	1.26 (0.07)	19.4 (1.6)	11.2 (1.2)	69.4 (4.7)	0.28 (0.02)

mixture of sterols, with cholesteroloids comprising 10.3 to 78.2% of the mixture, ergosteroids 4.9 to 43.0%, and stigmasteroids 7.2 to 60.1% (table S4). Moreover, rhizarian protists may produce C₃₀ sterols (24-*n*-propylcholesteroids) that can form a notable (up to ~20%) proportion of their total sterol content (37). By contrast, in most *Dickinsonia* and *Andiva* extracts, C₃₀ steroids were below detection limits. Thus, the steroid composition of dickinsoniids is markedly distinct from steroid distributions observed in Rhizaria, rendering a protozoan affinity of these fossils extremely unlikely. All animals—with rare exceptions, such as some demosponges and bivalve molluscs—are characterized by exclusive production of C₂₇ sterols (32, 33). The closest relatives of metazoans, *Choanoflagellata* and *Filasterea*, produce 90 to 100% and 84 to 100% of cholesterol, respectively, and contain up to 16% ergosteroids (34–36). Although the sterol composition of some choanoflagellates and filastereans falls within the range observed for *Dickinsonia* and

Andiva, they are unlikely precursor candidates because these groups are only ever represented by microscopic organisms, leaving a stem- or crown-group metazoan affinity as the only plausible phylogenetic position for *Dickinsonia* and its morphological relatives.

Molecular fossils firmly place dickinsoniids within the animal kingdom, establishing *Dickinsonia* as the oldest confirmed macroscopic animals in the fossil record (558 million years ago) next to marginally younger *Kimberella* from Zimnie Gory (555 million years ago) (37). However alien they looked, the presence of large dickinsoniid animals, reaching 1.4 m in size (38), reveals that the appearance of the Ediacara biota in the fossil record is not an independent experiment in large body size but indeed a prelude to the Cambrian explosion of animal life.

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ACKNOWLEDGMENTS

We thank E. Luzhnaya, A. Krasnova, A. Nagovitsyn, P. Rychkov, V. Rychkov, and S. Rychkov for their help with collecting Ediacaran fossils; E. Golubkova with organizing one of the field trips; P. Pringle and R. Taroza for laboratory support; and F. Not, C. Schmidt, R. Schiebel, P. De Deckker, S. Eggins, J. Pawlowski, S. S. Bowser, and M. Stuhr for rhizarian specimens. **Funding:** The study is funded by Australian Research Council grants DP160100607 and DP170100556 (to J.J.B.), Russian Foundation for Basic Research project 17-05-02212A (A.I. and I.B.), and the Max-Planck-Society (C.H.). I.B. gratefully acknowledges an

Australian Government Research Training Program stipend scholarship, and B.J.N. acknowledges a Geobiology fellowship of the Agouron Institute. **Author contributions:** I.B. designed the study and analyzed biomarkers from Ediacaran fossils; J.M.H. helped with biomarker analysis; I.B. and A.I. collected fossils; B.J.N., C.H., J.M.H., and J.J.B. analyzed modern Rhizaria; and I.B. and J.J.B. interpreted data and wrote the manuscript, with contributions from all authors. **Competing interests:** Authors declare no competing interests. **Data and materials availability:** All data required to understand and assess the conclusions of this research are available in the main text and supplementary materials.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6408/1246/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S6
Tables S1 to S4
References (39–55)

2 April 2018; accepted 6 August 2018
10.1126/science.aat7228

Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals

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Science **361** (6408), 1246-1249.
DOI: 10.1126/science.aat7228

Confirming the identity of early animals

The first complex organisms emerged during the Ediacaran period, around 600 million years ago. The taxonomic affiliation of many of these organisms has been difficult to discern. Fossils of *Dickinsonia*, bilaterally symmetrical oval organisms, have been particularly difficult to classify. Bobrovskiy *et al.* conducted an analysis using lipid biomarkers obtained from *Dickinsonia* fossils and found that the fossils contained almost exclusively cholesteroloids, a marker found only in animals (see the Perspective by Summons and Erwin). Thus, *Dickinsonia* were basal animals. This supports the idea that the Ediacaran biota may have been a precursor to the explosion of animal forms later observed in the Cambrian, about 500 million years ago.

Science, this issue p. 1246; see also p. 1198

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